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# Insect evolution toward aquatic habitats; reassessment of antennal sensilla in the water bug families Ochteridae, Gelastocoridae and Aphelocheiridae (Hemiptera: Heteroptera: Nepomorpha)

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## Abstract

The first comparative morphology study on antennal sensilla of Ochteridae, Gelastocoridae and Aphelocheiridae, carried out with the use of a scanning electron microscope, is provided. Our research hypothesis was: the antennal sensilla of the studied families reflect their different adaptations for use in aquatic habitats, while maintaining a common set of sensilla similar to other water bugs (Nepomorpha). Therefore, the number and placement of antennal sensilla of several species in the mentioned families were studied using scanning electron microscopy. Nine main types of mechano- chemo- and thermo-hygroreceptive sensilla were confirmed on their surface, including sensilla trichodea, chaetica, club-like, campaniformia, basiconica, coeloconica, plate-like, ampullacea and sensilla placodea multilobated. While seven of these were already documented in other species, two of them (sensilla plate-like and placodea multilobated) were yet to be documented on the antennae of Nepomorpha. All families display differences in the shape and length of antennae as well as among sensilla types. These findings support our hypothesis regarding differences in sensillar structures among families adapted differently to suitable niches. Differences between these families and previously studied nepomorph taxa (Neptoidea) were also documented. However, the general set of sensilla observed on the antennae of the studied species is very similar to the one documented in Neptoidea. Therefore, we confirmed our assumptions regarding similarities in antennal sensilla between the studied families and other nepomorph insects.

## Keywords

antennal sensilla – morphology – nepomorpha – Ochteridae – Gelastocoridae – Aphelocheiridae

## Introduction

Members of the true water bugs, or Nepomorpha have long attracted the attention of researchers due to the possession of diverse body structures and lifestyles. These nepomorphan insects, being predaceous (except most corixids, that may also be scavengers or consume algae), are one of the most specialized groups among heteropterans. The Nepomorpha are recognized as a group of secondarily aquatic bugs among the suborder of Heteroptera (Popov, 1971). Most remaining taxa in this infraorder are terrestrial, except the Gerromorpha, or semi-aquatic bugs (Polhemus et al., 1995; Schuh & Slater, 1995).

The water bugs currently classified as the Nepomorpha, include about 2000 species worldwide (Polhemus et al., 1995), with 13 families recognized in this infraorder (Nieser, 2002). By contrast, 11 families were distinguished by Chen et al. (2005) and were grouped differently in seven superfamilies (Hebsgaard et al., 2004; Brožek, 2014; Ye et al., 2020).

Evolutionary transitions of insects from terrestrial to aquatic habitats provide important insights into how their organismal traits have responded to major adaptive shifts (Crespo, 2011). Opportunities for documentation such inferences are limited, because many secondarily aquatic insect taxa are still lacking detailed morphological data.

The beginning of diversification of the whole nepomorphan group is estimated to have occurred in the late Permian (about 263 Ma) (Ye et al., 2020). It is certain, on the basis of fossils, that they existed during the mid-Triassic and are a divergence from the terrestrial group (Grimaldi & Engel, 2005). Important examples of Nepomorpha are represented

by some family groups: Ochteridae, Gelastocoridae, which are terrestrial/hydrophiine bugs, which comprise water margin inhabitants (China, 1955; Popov, 1971; Schuh & Slater, 1995; Papáček, 2001; Kment & Jindra, 2008), as well as Aphelocheiridae and the other remaining families (Nepidae, Belostomatidae, Corixidae, Naucoridae, Notonectidae, Pleidae and Helotrephidae) which live submerged in water (Polhemus & Polhemus, 1988).

Popov (1971) hypothesized that a proto-heteropteran terrestrial lineage gave rise, among others, to protoochterids that resulted in three main branches of aquatic bugs in the mid-Triassic period: The first branch was Nepoidea (Nepidae and Belostomatidae), the second was Corixoidea (Corixidae) and the third branch at first led to Ochteroidea and next to Naucoroidea, Notonectoidae and Pleoidea. The present study focuses on the sensillar system of the antennae in three particular families (Ochteridae, Gelastocoridae and Aphelocheiridae) which are considered suitable targets for studying the evolution of organismal traits resulting from multiple transitions between land and water.

The family Ochteridae consists of 80 species, and displays its highest diversity in tropical regions. The four-segmented antennae are easily visible because they extend over the head (Chen et al., 2005). In contrast with nepomorphan groups which are fully aquatic, Ochteridae are considered to be semi-aquatic (hydrophiine), or even riparian (Chen et al., 2005). They inhabit mossy rocks along streams, walls of waterfalls, sand banks and other edges of water reservoirs (Zettel & Lane, 2010). They are zoophagous and are believed to prey on small invertebrates such as dipteran larvae (Chen et al., 2005). Many members

of the Ochteridae are terrestrial and are often found at long distances from aquatic habitats (Ye et al., 2020).

Gelastocoridae consists of two subfamilies, Gelastocorinae and Nerthrinae (Todd, 1955). They all have four-segmented antennae concealed in groves beneath the eyes (Todd, 1955; Chen et al., 2005), not visible from the dorsal perspective. The Gelastocoridae are considered riparian or even terrestrial bugs (similar to Ochteridae), which distinguishes them from most Nepomorphan families in terms of habitat. Several species of *Nerthra* have even been collected far from water. At least three species have been found under water (La Rivers, 1953). However given the gelastocorids' habitat, this particularity is rather the exception. There is no documentation regarding their ability to fly. Some species even have fused hemelytra which makes them unable to fly (Chen et al., 2005). They are predatory bugs (Schuh & Slater, 1995) and have the ability to jump while hunting prey.

Aphelocheiridae, similar to the other taxa previously discussed, have four-segmented antennae. In contrast to Gelastocoridae, the antennae in Aphelocheiridae are easily visible, since they are not concealed. Species of *Aphelocheirus* are known for their ability to stay submerged underwater (Andersen & Weir, 2004), which is possible due to their plastron respiration system that also allows them to complete their entire life cycle underwater (Polhemus & Polhemus, 1988). They feed on immature forms of various aquatic insects such as Ephemeroptera and Trichoptera.

While there are no doubts about the classification of Gelastocoridae and Ochteridae – they both belong to the superfamily Ochteroidea (Štys & Jansson, 1988; Hebsgaard, 2004; Brožek, 2014; Ye et al., 2020) the systematic position of Aphelocheiridae in Nepomorpha is unclear. In previous classifications the taxon was a subfamily of Aphelocheirinae (Polhemus & Polhemus, 1988) within the

Naucoroidea, but later was elevated to family position (Štys & Jansson, 1988). Aphelocheiroidea, a new superfamily, was formed afterwards, consisting of two families, Aphelocheiridae and Potamocoridae (Hebsgaard, 2004), after which they were collapsed into a single family in the aforementioned superfamily (Brožek, 2014). A recent study gave conflicting results and Aphelocheiridae returned to Naucoroidea (Ye et al., 2020). Therefore, in this study we consider the morphology of sensilla on the family level and do not exclude Aphelocheiridae from belonging to any superfamily (Aphelocheiroidea or Naucoroidea).

Among sensory organs, the antennae usually have the highest concentration and diversity. External sensilla possess an external cuticular shaft of various sizes and shapes, and a socket or joint that anchors the process in the surrounding epidermis, so they present many different morphologies adapted to their modality. They play a mechanical, chemosensory and thermo-hygroreceptive function (Slifer, 1970; Altner & Prillinger, 1980; Hallberg & Hansson, 1999; Zacharuk, 1980; Shields, 2010).

Sensillar systems are especially important for aquatic insects which live in dense, dark, highly complex habitat conditions or species with poor vision capabilities (Brönmark & Hanssons, 2000; Wisenden, 2000). Moreover, in aquatic insects, the distinction between taste and olfaction is vague, but is still used based on the structure and particular location of the sensilla, or behavioral response (Zacharuk, 1980; Crespo, 2011).

Until now, several types of labial sensilla (sensilla trichodea, chaetica, squamiformia, basiconica, club-like, paddle-like, cupola-shaped, and peg sensilla) have been described in numerous species of Nepomorpha (Brožek, 2013, 2014). More general research has also been done on the basal shapes of the antennae and distributions of some sensilla in representatives of nepomorphan families (Popov, 1971; Schuh & Slater, 1995; Chen et al., 2005).

Moreover, a small amount of data about the morphology and distribution of more visible sensilla (trichodea or basiconica) on the surface of antennae of *Notonecta glauca*, *Plea leachi*, *Nepa cinerea*, *Ranatra linearis* and *Sigara striata* has been presented by Chaika & Sinitsina (1999), although the possible functions of the sensilla have not been indicated. However, newer morphological studies of antennal sensilla from species of Nepoidea, performed by Nowińska & Brożek (2019), have shown some inconsistencies in comparison to data from Chaika & Sinitsina (1999).

Although some papers (mentioned above) have shed light on the antennal structures and reception of environmental stimuli in some nepomorphan species, the understanding of the olfactory system in water bugs is still poor. Limited information on morphology and physiology is available, for a small number of species. The identification and description of antennal sensilla, through the use of scanning electron microscopy (SEM), for a comprehensive understanding of the sensory systems of the antennae, was performed only for a few Nepoidea species (Nowińska & Brożek, 2019).

We expect that the antennal sensilla of studied species from these families differ, because of their various adaptations to the water habitat. No studies of fine morphology and ultrastructure have been performed so far on these representatives of the families.

The research hypothesis is: the antennal sensilla of the studied families reflect their different adaptations for use in aquatic habitats, while maintaining a common set of sensilla similar to other water bugs (Nepomorpha).

Therefore, the aim of this study is to examine the morphological diversity and distribution of sensilla on the antennae, assign probable functions and compare them with homologous structures observed in other nepomorphan groups, as well as other terrestrial and semi-aquatic heteropteran groups.

## Materials and methods

The material was obtained from the collections of the Natural History Museum in Vienna, Zoological Museum of the State Moscow University and Hungarian Natural History Museum in Budapest. Additional species of *Nerthra* and *Gelastocoris* have been donated by Ping-ping Chen. All specimens have been cleaned in an ultrasound cleaner, the antennae have been dissected, dried in ethanol, mounted, sputtered with gold or chromium and observed with the use of the scanning electron microscopes Phenom XL and Hitachi UHR FE-SEM SU 8010 in the scanning microscopy laboratory of the Faculty of Natural Science, Institute of Biology, Biotechnology and Environmental Protection of Silesian University in Katowice. We follow the terminology and classification reported in other papers on antennal sensilla of insects (Altner & Prillinger, 1980; Nowińska & Brożek, 2019).

The antennae of eight species from three families have been studied:

- Aphelocheiridae:** *Aphelocheirus aestivalis*  
(Fabricius, 1803)  
Obtained from Hungarian Natural History Museum  
Label data: Seine bei Rouen, Gallia, coll. Horvath
- Ochteridae:** *Ochterus marginatus*  
(Latreille, 1804)  
Obtained from Hungarian Natural History Museum  
Label data: Japan, Okayama  
H. Sauter, det. P. Chen
- Gelastocoridae:** Gelastocorinae:  
*Gelastocoris* sp.  
Obtained from Zoological Museum of the State Moscow University  
Species identified in the Museum, the place of collection cannot be

confirmed

***Gelastocoris flavus flavus***

(Guérin-Méneville, 1835)

Obtained thanks to donation from Dr Ping-ping Chen

Label data: Bronopondo, road to Brownsweeg, ponds, leg. N. Nieser SN229/30, det. P. Chen

Nerthrinae:

***Nerthra femoralis***

(Montandon, 1899)

Obtained from Natural History Museum in Vienna  
Species identified in the Museum, the place of collection cannot be confirmed***Nerthra fuscipes***

(Guérin-Méneville, 1843)

Obtained from Hungarian Natural History Museum  
Label data: Mexico, Procopp***Nerthra ampliata***

(Montandon, 1899)

Obtained from Hungarian Natural History Museum  
Label data: N. Guinea, Biro 1900, Stephansort, Astrolabe Bay***Nerthra ranina***

(Herrich-Schäffer, 1853)

Obtained thanks to donation from Dr Ping-ping Chen  
Label data: Argentina, det. Nieser & Chen

shorter (130 and 120  $\mu\text{m}$ ) and wider than the other two (230 and 270  $\mu\text{m}$ ). Whole antennae are visibly covered with hair-like sensilla (fig. 1a). The antennae of *Gelastocoris* and *Nerthra* are visibly thicker. In both, the last antennomer remains the longest (around 300  $\mu\text{m}$  in *Gelastocoris* and around 400/500  $\mu\text{m}$  in *Nerthra*) but there is a difference in the length of the third antennomer. In *Gelastocoris* it is much shorter (170  $\mu\text{m}$ ) than in *Nerthra* (around 200–300  $\mu\text{m}$ ), but in both cases the third antennomer is the shortest (figs 2a, 4b). In *Aphelocheirus* we observe around 1 mm long and thin four-segmented antennae. The first two antennomers (scapus and pedicel) are shorter (around 150 and 170  $\mu\text{m}$ ), while the other two (antennomers of flagellum) are visibly longer (300 and 490  $\mu\text{m}$ ). The antennae are rather smooth, with only some groups of thick sensilla visible on the surface (fig. 5a).

***Antennal sensilla***

In this study, based on morphological characteristics, nine main types of sensilla have been found (sensilla trichodea, chaetica, club-like, campaniformia, basiconica, coeloconica, ampullacea, plate-like and multilobated) (fig. 6). Some of these types have been described in other insects (McIver, 1975; Zacharuk, 1980), as well as in some heteropteran insects (Brożek, 2013, 2014; Nowińska & Brożek, 2019). Sensilla trichodea, club-like, campaniformia and basiconica (subtype 1), because of their flexible sockets, are believed to play a mechanoreceptive function. Sensilla basiconica (subtype 2, 3 and 4) function as chemoreceptive sensilla given their porous surface and inflexible socket. Pores on the surface of these sensilla indicate an olfactory function. Another function is thermo-hygroreception and it is performed by sensilla ampullacea and sensilla coeloconica. Taking into account the external morphological features (shape and build) of sensilla plate-like and multilobated, we assume that they

**Results*****Gross morphology of the antennae***

Differences in the shapes of the species' antennae have been observed. The length of the thin antennae of *Ochterus* is approximately 750  $\mu\text{m}$ . The first two antennomeres are



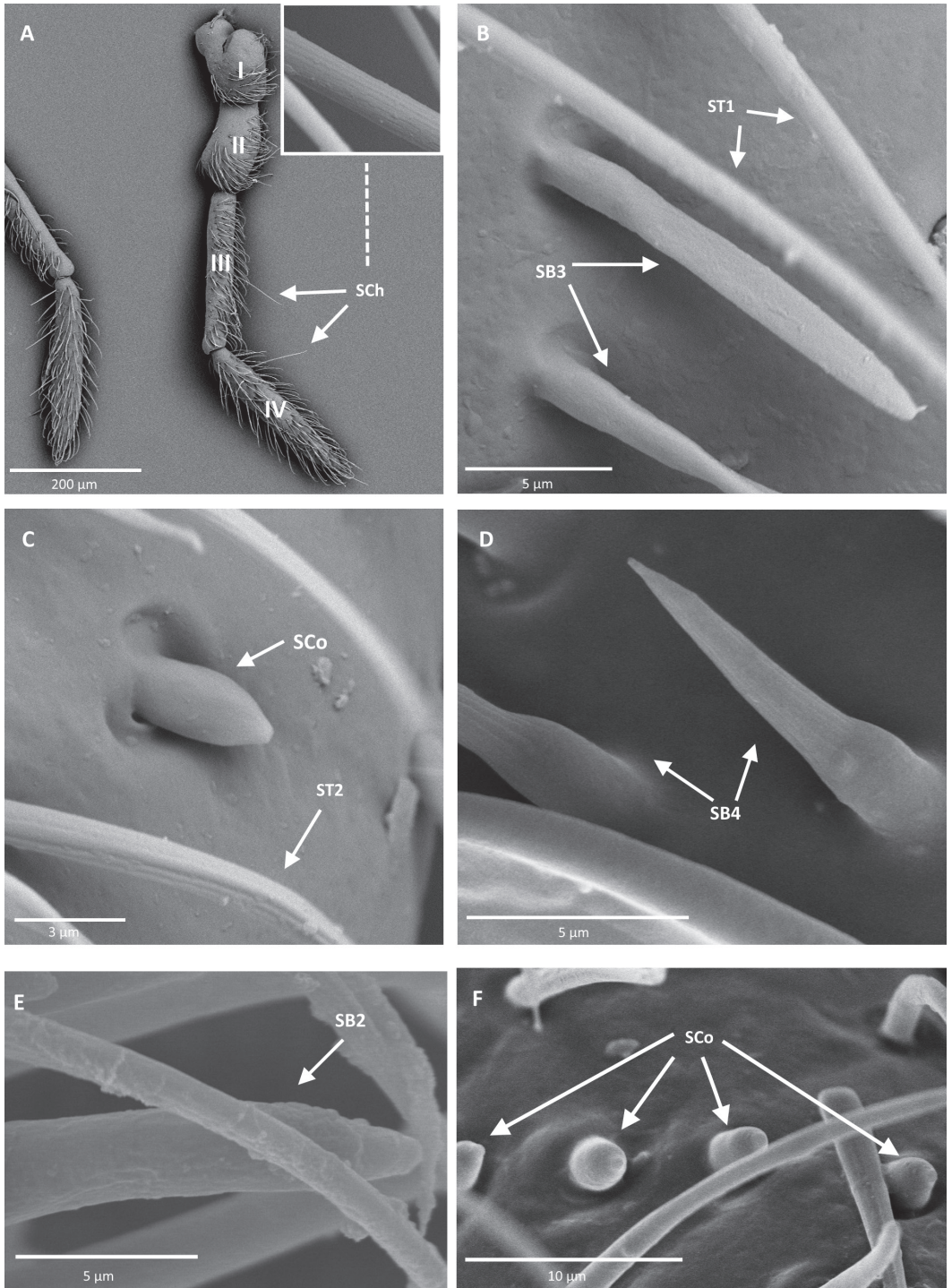


FIGURE 1 *Ochterus marginatus*; Sch, sensilla chaetica; SB, sensilla basiconica; ST, sensilla trichodea; SCo, sensilla coeloconica.

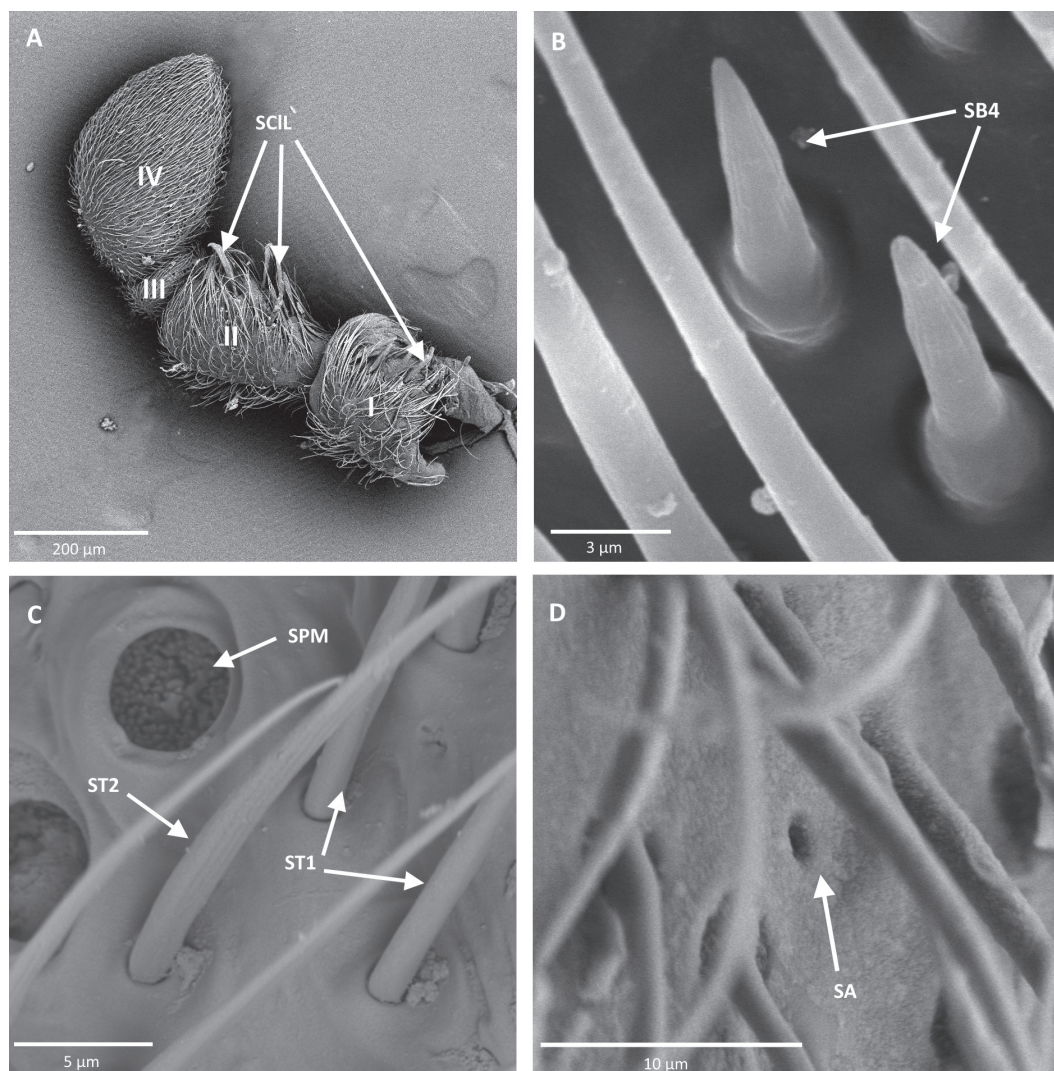


FIGURE 2 A, B, *Gelastocoris flavus flavus*; C, D, *Gelastocoris* sp.; SCIL, sensilla club-like; SA, sensilla ampullacea; ST, sensilla trichodea; SPM, sensilla placodea multilobated; SB, sensilla basiconica.

perform a chemoreceptive function. Morphological features and distribution of antennal sensilla are summarized in table 1 and the distribution of sensilla on the antennae is reported in specific figures (figs 1a, 2a, 4b, 5a).

Sensilla trichodea – these are usually long sensilla resembling hair, tapered from the base to the tip and curved towards the antennal shaft or they are nearly straight hairs. Frequently, they occur in large numbers, less often as a single hair. They are embedded

into flexible sockets. According to the surface shape and length, two subtypes have been distinguished:

1. Sensilla trichodea (ST<sub>1</sub>) – these are long sensilla trichodea, blunt-tipped straight hairs with a smooth surface. They are usually numerous on the surface of the antennae and have been found in all of the studied species (figs 1b, 2c, 4f).
2. Sensilla trichodea (ST<sub>2</sub>) – these are long sensilla trichodea, blunt-tipped and



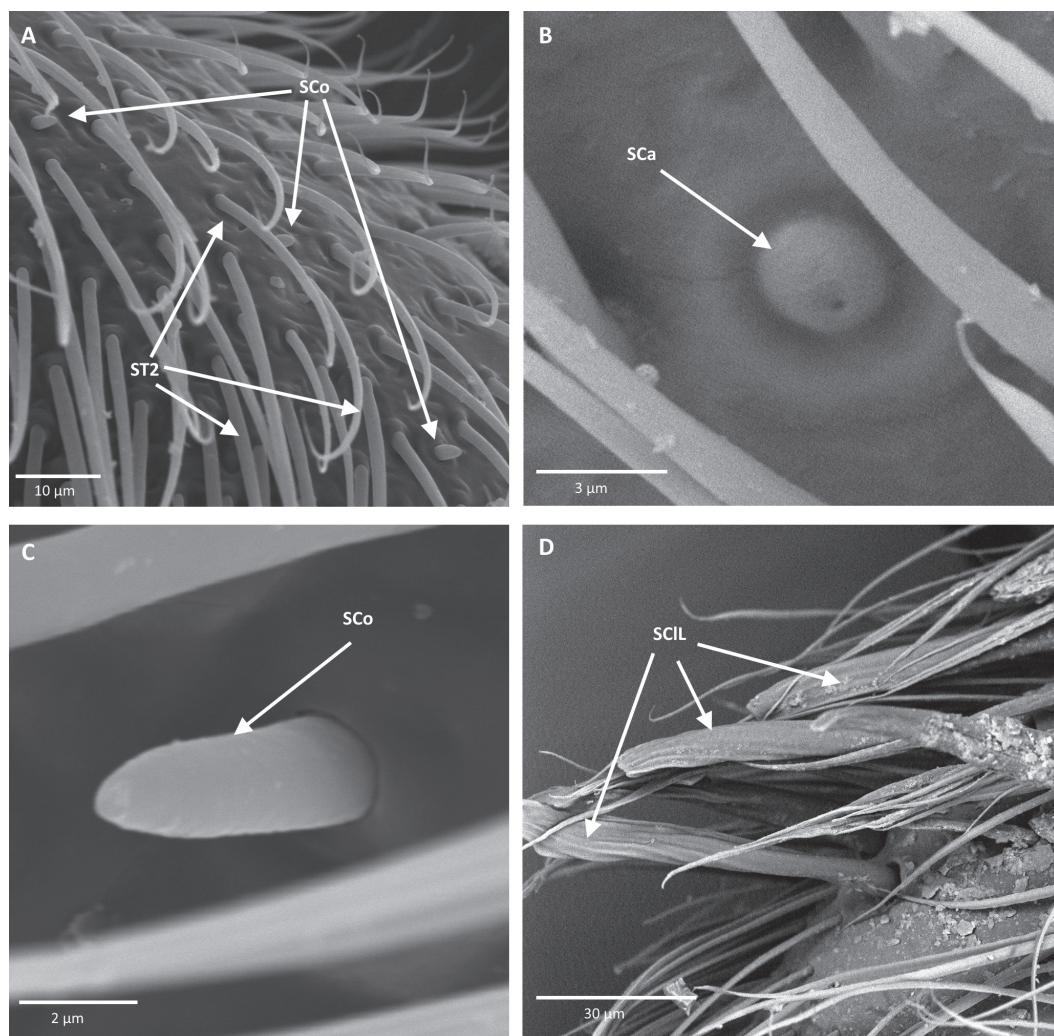


FIGURE 3 *Gelastocoris flavus flavus*; ST, sensilla trichodea; SCo, sensilla coeloconica; SCa, sensilla campaniformia; SCIL, sensilla club-like.

curved towards the antennal shaft, with a ribbed surface. They are slightly wider than ST<sub>1</sub>. They have been found in *Ochterus*, *Gelastocoris* and *Nerthra* on all of the antennomeres (figs 1c, 2c, 3a).

Sensilla chaetica (SCh) – these sensilla are more pronounced than sensilla trichodea, mainly in length and width. They are ribbed and inserted in flexible sockets, rising much higher than sensilla trichodea, which makes them well visible. They have been found in

*Ochterus* on all antennomeres, where they occur singularly and in *Nerthra ampliata* as a single sensillum on the first antennomere (figs 1a, 4d).

Sensilla club-like (SCIL) – these sensilla are more pronounced and thicker than sensilla trichodea. They are ribbed, flattened and rise from flexible sockets. They occurred in Ochteridae. In *G. flavus* and *Gelastocoris sp.* on the 1<sup>st</sup> and 2<sup>nd</sup> antennomeres, these sensilla occur in groups and in *Nerthra femoralis* on

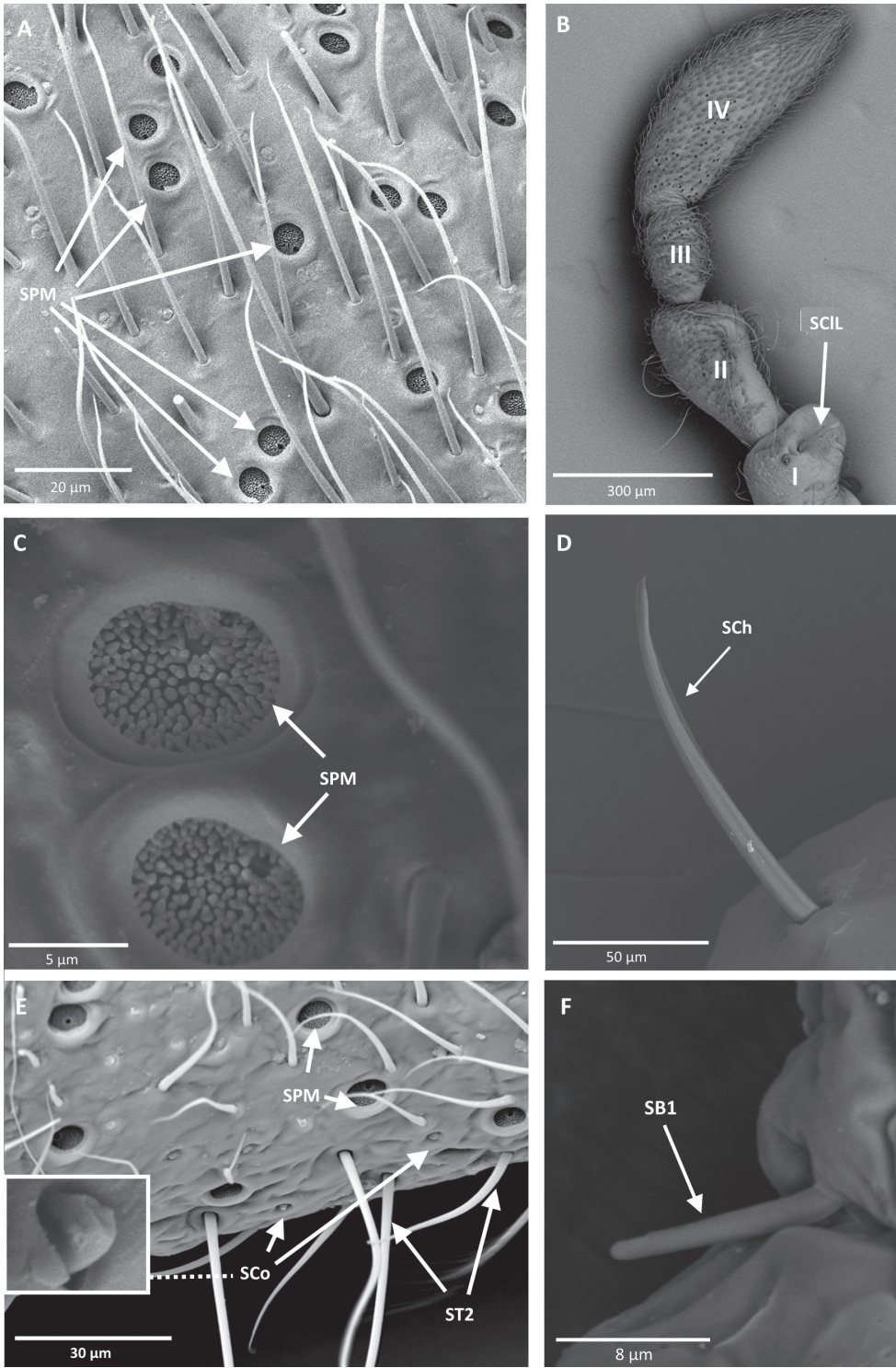


FIGURE 4 A, B, C, E, *Nerthra femoralis*; D, *Nerthra ampliata*; F, *Nerthra fuscipes*; SPM, sensilla placodea multilobata; SCIL, sensilla club-like; SCh, sensilla chaetica; SCo, sensilla coeloconica; ST, sensilla trichodea; SB, sensilla basiconica.



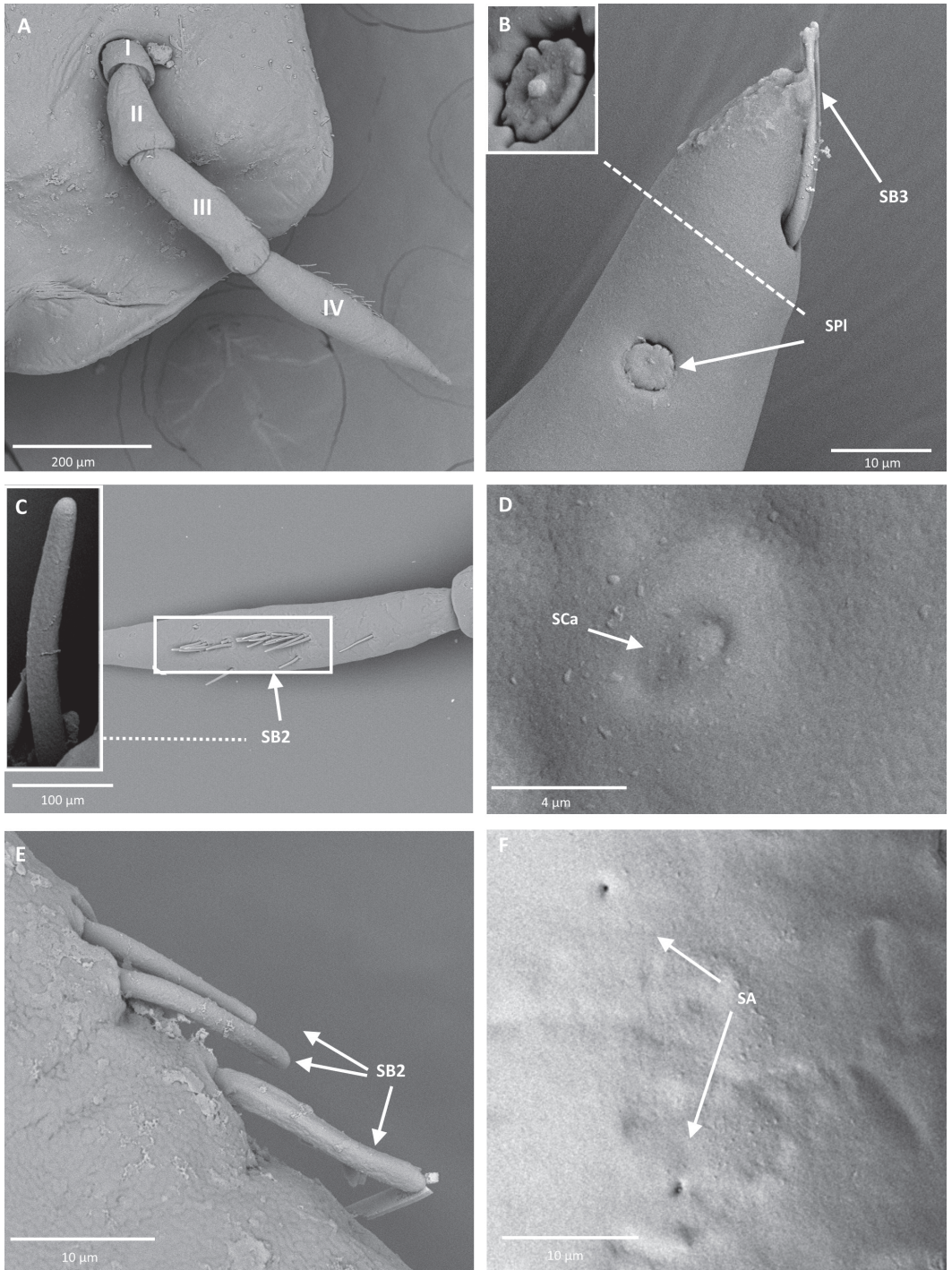


FIGURE 5 *Aphelocheirus aestivalis*; SPL, sensilla plate-like; SB, sensilla basiconica; SCa, sensilla campaniformia; SA, sensilla ampullacea.

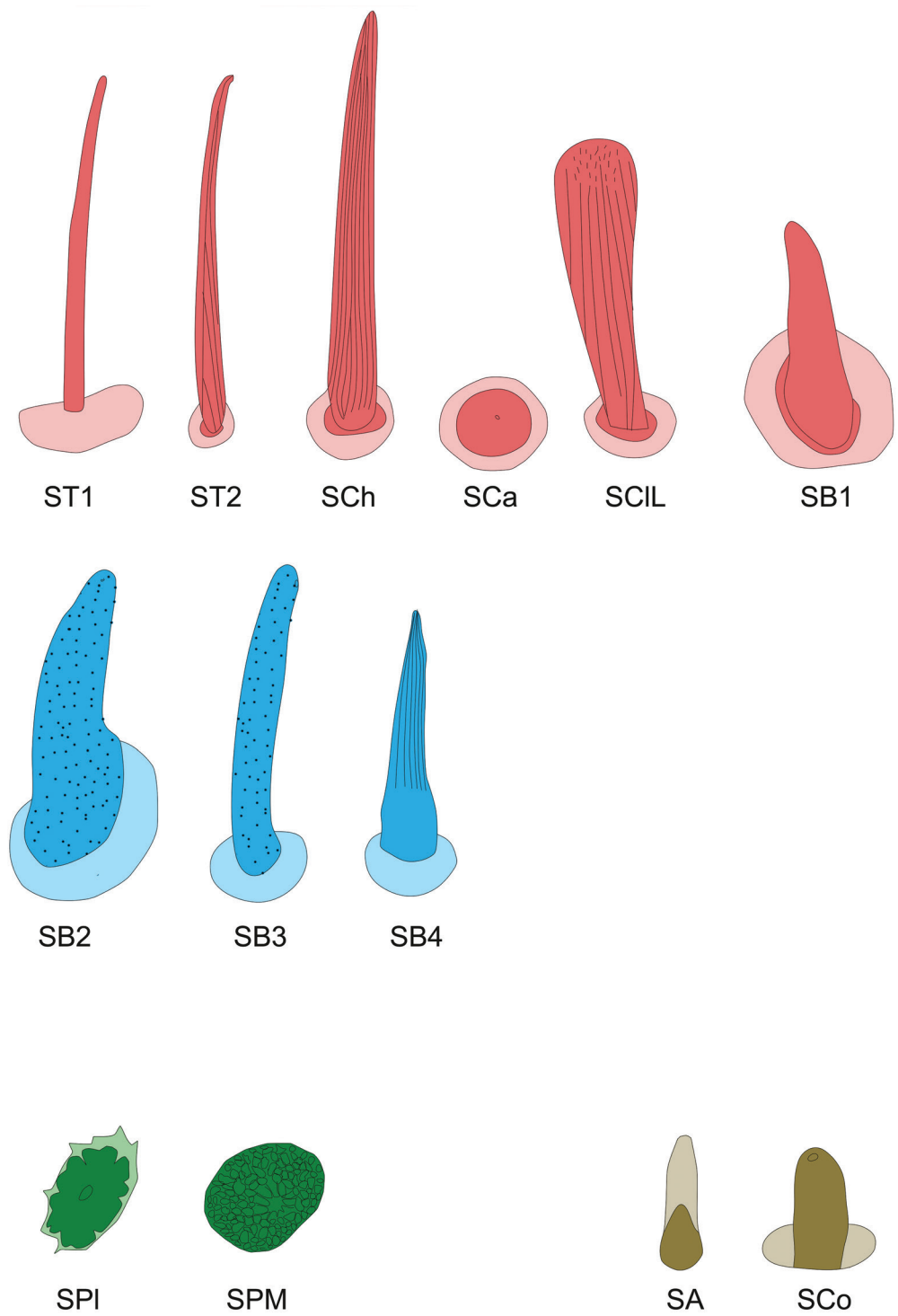


FIGURE 6 Shapes of sensilla; ST, sensilla trichodea; SCh, sensilla chaetica; SCa, sensilla campaniformia; SCIL, sensilla club-like; SB, sensilla basiconia; SPI, sensilla plate-like; SPM, sensilla placodea multilobated; SA, sensilla ampullacea; SCo, sensilla coeloconica.

TABLE 1 The presence of sensilla types on the antennae, according to their function and their arrangement

Species	MS	CHS	THS	UNF (olfactory?)	sensilla on antennomeres (anm)	Sensilla quantity
<i>Ochterus marginatus</i>	ST <sub>1</sub> ST <sub>2</sub> SCh SB <sub>1</sub>	SB <sub>2</sub> SB <sub>3</sub> SB <sub>4</sub>	SA SCo		ST all anm SCh all anm SB <sub>2</sub> 4 <sup>th</sup> anm SB <sub>3</sub> the 3 <sup>rd</sup> and 4 <sup>th</sup> anm SB <sub>4</sub> 2 <sup>nd</sup> and 4 <sup>th</sup> anm SCo 3 <sup>rd</sup> and 4 <sup>th</sup> anm	ST numerous SCh singularly SB <sub>2</sub> few SB <sub>3</sub> numerous SB <sub>4</sub> singularly or few SCo singularly or few
<i>Gelastocoris sp.</i>	ST <sub>1</sub> ST <sub>2</sub> SCIL SB <sub>1</sub>	SB <sub>2</sub> SB <sub>3</sub> SB <sub>4</sub>	SA	SPM	ST all anm SCIL 1 <sup>st</sup> and 2 <sup>nd</sup> anm SB <sub>2</sub> 2 <sup>nd</sup> -4 <sup>th</sup> anm SB <sub>3</sub> last anm SB <sub>4</sub> 2 <sup>nd</sup> -4 <sup>th</sup> anm SPM 3 <sup>rd</sup> and 4 <sup>th</sup> anm	ST numerous SCIL occur in groups SB <sub>2</sub> singularly SB <sub>3</sub> numerous SB <sub>4</sub> singularly SPM numerous
<i>Gelastocoris flavus flavus</i>	ST <sub>1</sub> ST <sub>2</sub> SCa SCIL SB <sub>1</sub>	SB <sub>2</sub> SB <sub>4</sub>	SA SCo	SPM	ST all anm SCIL 1 <sup>st</sup> and 2 <sup>nd</sup> anm SB <sub>2</sub> 2 <sup>nd</sup> -4 <sup>th</sup> anm SB <sub>4</sub> 2 <sup>nd</sup> -4 <sup>th</sup> anm SCo 2 <sup>nd</sup> anm SPM 3 <sup>rd</sup> and 4 <sup>th</sup> anm	ST numerous SCIL occur in groups SB <sub>2</sub> singularly SB <sub>4</sub> occur in groups / line SCo few SPM numerous
<i>Nerthra femoralis</i>	ST <sub>1</sub> ST <sub>2</sub> SCa SCIL SB <sub>1</sub>	SB <sub>2</sub>	SA SCo	SPM	ST all anm SCIL 1 <sup>st</sup> anm SB <sub>2</sub> 2 <sup>nd</sup> -4 <sup>th</sup> anm SCo 4 <sup>th</sup> anm SPM 3 <sup>rd</sup> and 4 <sup>th</sup> anm	ST numerous SCIL single SB <sub>2</sub> singularly SCo in groups / singularly SPM numerous
<i>Nerthra fuscipes</i>	ST <sub>1</sub> ST <sub>2</sub> SB <sub>1</sub>	SB <sub>2</sub>	SA	SPM	ST all anm SB <sub>2</sub> 2 <sup>nd</sup> -4 <sup>th</sup> anm SPM 3 <sup>rd</sup> and 4 <sup>th</sup> anm	ST numerous SB <sub>2</sub> singularly SPM numerous
<i>Nerthra ampliata</i>	ST <sub>1</sub> ST <sub>2</sub> SCh SB <sub>1</sub>	SB <sub>2</sub>	SA	SPM	ST all anm SCh 1 <sup>st</sup> anm SB <sub>2</sub> 2 <sup>nd</sup> -4 <sup>th</sup> anm SPM 3 <sup>rd</sup> and 4 <sup>th</sup> anm	ST numerous SCh single SB <sub>2</sub> singularly SPM numerous
<i>Nerthra ranina</i>	ST <sub>1</sub> ST <sub>2</sub> SB <sub>1</sub>	SB <sub>2</sub> SB <sub>4</sub>	SA SCo	SPM	ST all anm SB <sub>2</sub> 2 <sup>nd</sup> -4 <sup>th</sup> anm SB <sub>4</sub> 2 <sup>nd</sup> and 4 <sup>th</sup> anm SCo 4 <sup>th</sup> anm SPM 3 <sup>rd</sup> and 4 <sup>th</sup> anm	ST numerous SB <sub>2</sub> singularly SB <sub>4</sub> singularly SCo few SPM numerous
<i>Aphelocheirus aestivalis</i>	ST <sub>2</sub> SCa	SB <sub>2</sub> SB <sub>3</sub>	SA	SPL	ST 3 <sup>rd</sup> anm SB <sub>2</sub> 3 <sup>rd</sup> and 4 <sup>th</sup> anm SB <sub>3</sub> tip of the 4 <sup>th</sup> anm SPL 4 <sup>th</sup> anm	ST singularly SB <sub>2</sub> in groups SB <sub>3</sub> single SPL numerous



the 1<sup>st</sup> antennomere, single sensillum club-like have been found (figs. 2a, 3d, 4b).

Sensilla campaniformia (SCa) – these are round plates with a single pore, embedded in flexible sockets. They have been documented only in a few species. However, this type is common for all insects so we believe it is also present in other species studied (figs 3b, 5d).

Sensilla basiconica – these are long structures, thick and curved or tapered at the tip. They are inserted in inflexible sockets. We have distinguished four subtypes of these sensilla:

1. Sensilla basiconica (SB1) – this kind of sensilla is responsible for mechanoreception. It is present between the antennomeres and is being stimulated by the movement of each antennomere. It is a common type of sensilla on insects' antennae (fig. 4f).
2. Sensilla basiconica (SB2) – these are sensilla basiconica with the same width along the whole surface and slightly rounded tip. They bear pores along the whole surface. SB2 have been found in all of the studied species. In *Aphelocheirus* on the 3<sup>rd</sup> and 4<sup>th</sup> antennomere, sensilla occur in groups. In *Gelastocoris* and *Nerthra* on the 2<sup>nd</sup>-4<sup>th</sup> antennomere, sensilla occur singularly. In *Ochterus* the most visible and significant are sensilla at the tip of the 4<sup>th</sup> antennomere – one sensillum at the tip is surrounded by a few other SB2 (figs 1e, 5c, e).
3. Sensilla basiconica (SB3) – these are porous sensilla basiconica, long and flattened along the whole length. They have been found in *Ochterus* on the third and fourth antennomere, in *Gelastocoris* on the last antennomere and in *Aphelocheirus* as a single sensillum at the tip of the antenna (figs 1b, 5b).
4. Sensilla basiconica (SB4) – these are sensilla basiconica that are smooth at the base and tapered at the tip. The rest

of the surface is ribbed and porous. They are wider at the base and tapered along their length. These sensilla have been found in *Ochterus marginatus* on the 2<sup>nd</sup>-4<sup>th</sup> antennomere, where sensilla occur singularly or a few of them are spread on the surface. In *Gelastocoris sp.* on the 2<sup>nd</sup>-4<sup>th</sup> antennomere, sensilla occur singularly and in *Gelastocoris flavus flavus* they occur in groups or a few sensilla are arranged in line along the antennomere. These sensilla have also occurred singularly in *Nerthra ranina* on the 2<sup>nd</sup> and 4<sup>th</sup> antennomere. They are straight or bent towards the surface of the antenna (figs 1b, 2b).

Sensilla coeloconica (SCo) – these are peg in pit sensilla, embedded in shallow open cavities of the cuticle. They are embedded in inflexible sockets. They are nonporous and occur among sensilla trichodea. These sensilla have been found in *Ochterus* on the 3<sup>rd</sup> and 4<sup>th</sup> antennomere, where sensilla occur singularly, in groups or in a line of a few sensilla, *Gelastocoris flavus flavus* where few sensilla have been observed on the 2<sup>nd</sup> antennomere, *Nerthra femoralis* on the base and near the tip of the 4<sup>th</sup> antennomere, where sensilla occur in groups or singularly and in *Nerthra ranina* where few sensilla have been found on the 4<sup>th</sup> antennomere (figs 1c, f, 3a, c, 4e).

Sensilla plate-like (SPl) – these are round sensilla, with uneven edges. They occur only on the distant half of the 4<sup>th</sup> antennomere of *Aphelocheirus* and are more or less evenly distributed (fig. 5b).

Sensilla ampullacea (SA) – these are peg in pit sensilla with an external opening, which is cuticular and round, and in which no peg is visible because it is set internally at the bottom of a tube. Sensilla ampullacea rise from inflexible sockets. Single structures have been found in all of the studied species, in different locations throughout the antennae (figs 2d, 5f).

Sensilla placodea multilobated (SPM) – these are round cavities with small oval protuberances, that do not extend beyond the cuticular surface. They have been observed in *Nerthra* species and *Gelastocoris* on the 3<sup>rd</sup> and 4<sup>th</sup> antennomere, distributed on the whole surface of the antennomere (figs 2c, 4a, c).

## Discussion

This paper summarizes our morphological studies of the external antennal sensilla in three families of Nepomorpha, performed with the use of a scanning electron microscope. This study is important for the continuation of other morphological studies on the nepomorphan taxa and suggests possible functions of sensilla based on their morphology and distribution on the antennae. Similar studies have already been done in two other families – Belostomatidae and Nepidae (Nowińska & Brożek, 2019). More general research concerning the shapes of antennae and general occurrence of sensilla on the surface has been carried out by Popov (1971), Schuh & Slater (1995) and Chen et al. (2005). During these studies, nine morphological types of sensilla have been observed and their probable functions have been indicated. Sets of sensilla were compared within the studied families, as well as with other nepomorphan families, semi-aquatic bugs (Gerromorpha) and other heteropteran species.

### *Sensilla types*

The antennae of insects include many elementary sensilla, and they are treated as a complex multimodal insect organ (Chapman, 1998).

The morphological analysis of antennal sensory organs of the studied families (Ochteridae, Gelastocoridae and Aphelocheiridae) shows the presence of different sets of sensilla, forming three basal sensory systems:

olfactory, tactile (mechanoreception) and thermo-hygroreceptive systems. The first system is composed by sensilla with wall pores (sensilla basiconica, plate-like sensilla and probably sensilla placodea multilobated). The second system – mechanoreception – includes different sensilla trichodea and chaetica as well as campaniformia and cone-shaped proprioceptive sensilla, all placed in flexible sockets and bearing characteristic nonporous surfaces. The hygro-thermoreceptive sensory system is represented by nonporous peg in pit sensilla (ampulacea) and sensilla coeloconica. All such sensilla are common in most insects (Chapman, 1998) as well as in nepomorphan nepid taxa (Nowińska & Brożek, 2019) and in the currently studied families. However, their different polymorphic shapes constitute different subtypes, which may be assigned to different functions depending on their morphology and receptor's structures.

### *Olfactory sensilla*

In Ochteridae (*Ochterus marginatus*) the olfactory system includes three subtypes of sensilla basiconica (SB2, SB3 and SB4) which are similar in both genera of Gelastocoridae (Gelastocorinae; *Gelastocoris* sp., *G. flavus*) and *Nethra* (Gelastocoridae: Nethrinae). All examined species of Gelastocoridae were found to share numerous sensilla placodea multilobated (SPM). A slight difference in the aforementioned taxa was observed in the olfactory system of Aphelocheiridae (*Aphelocheirus aestivalis*), in which only two types of sensilla basiconica (SB2 and SB3) were observed, albeit in fewer numbers, as well as several plate-like sensillum (SP1). In the present study, all sensilla categorized as belonging to the olfactory system meet the standards regarding olfactory sensilla previously morphologically documented in other insects by many authors (Altner & Prillinger, 1980; Chapman, 1998; Shields, 2010; Nowińska & Brożek, 2017, 2019).

At this stage of research, it is difficult to clearly indicate the extent of olfactory perception in these bugs, as they are mainly associated with the aquatic environment. The current data shows evident differences between relevant taxa, because sensilla SB3 or SB4 are present only in some of the studied species (table 1). SB3 is thin walled with many pores in contrast to the thick, grooved and porous sensilla SB4. Both types (SB3 and SB4) of olfactory sensilla were recognized in many insect groups (Zacharuk, 1980; Brézot et al., 1997; Ahmad et al., 2016). It is significant that SB4 was recognized in taxa related to Ochteridae and Gelastocoridae. SB4 is only documented in one *Nertha* species. In turn, SB3 is pointed in *Ochterus*, *Gelastocoris* and *Aphelocheirus*, but probably absent in *Nethra* species. Such differences in sensilla sets may imply the specific reception of chemical compounds. Analyzing the distribution and number of olfactory sensilla on antennae in the particular taxa examined, several SB2, SB3 and SB4 were found on the penultimate and last antennomeres (table 1) with the exception of *Aphelocheirus*, in which several SB2 occurred in groups on the penultimate and last antennomere, while SB3 was singularly located at the end of the last antennomere. In contrast, the presence of SB2 (thin walled multiporous) in all tested species can point to a monofunctional sensillum, probably responsible for the diagnosis of water chemistry.

Sensilla placodea multilobated (SPM) are found only in Gelastocoridae species and another type – plate like (SPL) – only in Aphelocheiridae. The latter type is distributed on the last antennomere along its length and is believed to be a chemoreceptive sensillum. Moreover, this shape of sensillum has not been observed in Ochteridae. The expected characteristic pores are impossible to observe on the multilobated sensilla of gelastocorids and plate-like in aphelocheirid species, due to the pores' probable small size. However, this

caveat does not exclude the sensilla's chemoreceptive function. These taxa, especially Aphelocheiridae, prefer stable water habitats (Andersen & Weir, 2004). Particular features, such as the cuticle without pores in chemosensory sensilla, were found in other water-living arthropods, thus reflecting a possible adaptation to the aquatic habitat (Gaino & Rebora, 1999). Probably, these sensilla are highly specific for the mentioned taxa and responsible for specific behavior.

Structures similar to sensilla placodea multilobated have been discovered on heteropterans' bodies and described as sieve-pores (Cobben, 1978) or cuticular peg-plates (Andersen, 1982; Andersen & Weir, 2004). However, the aforementioned authors did not identify any pores. Essentially, there is no clear information on whether these structures are glandular or sensorial. In the present study, the structures "sensilla placodea multilobated" are numerous and present on the antennae only in gelastocorid species. According to Slifer (1970), such grouped pegs in caves can be associated with an olfactory role, perceiving long distance stimuli. We observe significant discrepancies in chemical information detection sensilla, which are highly sensitive, due to aquatic insects's various adaptations to help in foraging, mating, reproduction, and assessment of predatory risk (Yee, 2014).

A fundamental prerequisite for nepomorphans and other aquatic insects is to be able to receive sensory cues in two very different biotopes during the immature and the adult stage, respectively. Olfactory systems consisting of different shaped sensilla basiconica (subtypes 2, 3) and coeloconica (subtypes 1, 2, 3) were also distinguished in other nepomorph taxa (Nepidae and Belostomatidae) (Nowińska & Brożek, 2019). However, the placoid-shaped olfactory sensilla did not occur. An important feature is the presence of a common type of olfactory sensillum basiconicum SB2 in all previously studied Nepoidea

(Nowińska & Brożek, 2019), as well as in all of the presently studied species. The occurrence of other different types of olfactory sensilla in Nepoidea is more characteristic for particular genera and species.

Generally, chemoreception in aquatic insects is the perception, via gustatory sensilla, of chemicals in an aqueous solution. If the insects are airborne, the chemicals are perceived by olfactory sensilla. Behavioral studies on the diving beetle *Laccophilus maculosus* showed that in the air, these beetles responded to about 10% of the concentration required to produce a similar response in water. A similar study pointed out that multiporous sensilla on the antennae of the diving beetle *Graphoderus occidentalis* are probably olfactory, but may also be sensitive to lower concentrations of chemicals in both air and water. It might indicate that the sensing of odors on both media is based on similar molecular and physiological processes (Jensen & Zacharuk, 1992). It has also been reported that the great diving beetle *Dytiscus marginalis* (Linnaeus, 1758) has a very well developed chemoreceptive sensilla located on the antennae (odor) or maxillary and labial palpi (taste), which are critical for detecting potential food (Yee, 2014).

#### Mechanoreceptive sensilla

The study of insect's mechanoreceptive sensilla has a long history. The most obvious peripheral sense organs are the numerous cuticular hairs on the insects' bodies and appendages, called setae, which are a type of mechanoreceptive sensilla. McIver (1975) and others classified a variety of sensilla and inferred their functions from general observations on the insects' behaviours and on the structure and topography of the sensilla. In this way, it was determined that setiform/hairform sensilla could monitor touch and indicate the flexion of joints; that campaniform sensilla could register bending of the cuticle,

and that the curiously modified setiform sensilla of *Nepa* served as static organs under water (Chapman, 1998). The mechanoreception system of the antennae in the studied aquatic bug species is represented by trichoid sensilla of different shapes. Many trichoid sensilla are fine enough to detect air vibrations (Shields, 2010). Thus, these sensilla are numerous in terrestrial and semi-aquatic bugs (Gonzaga-Segura et al., 2013; Nowińska & Brożek, 2018). Also, aquatic taxa can detect vibrations by using hair sensilla on the surface of water or while submerged. Hair sensilla (trichoid sensilla) are considered to be the structure from which all other types of sensilla are derived (McIver, 1970). They may appear as thick, hair-like or flattened structures (chaetica, club-like) or very fine hairs. Some of such hairs have peg-like or cone-like shapes. The present data shows mechanoreceptive sensilla in the three studied families as being composed of trichoid sensilla thin and smooth (ST<sub>1</sub>), slightly thick and ribbed (ST<sub>2</sub>) and thick and ribbed (chaetica, club-like) (Sch, SCIL). All of these types of sensilla are numerous in representatives of Ochteridae and Gelastocoridae and less numerous in Aphelocheiridae and represent similar patterns of distribution. In *Aphelocheirus*, however, they were observed singularly and the types of mechanoreceptive sensilla were very limited on the antennomeres in comparison with the other nepomorphans (Nepidae and Belostomatidae), which also prefer the underwater life-style. Probably, the absence of long mechanoreceptive sensilla on the antennal surface in *Aphelocheirus* might be an adaptation to the type of environment. The antennae are situated on the head without any physical protection from environmental stressors, therefore not concealed in grooves beneath the eyes as observed in Gelastocoridae or Nepoidea (Popov, 1971; Nowińska & Brożek, 2019). In Nepoidea, there is a great morphological diversity when it comes to mechanoreceptive sensilla, where

nine types were recognized, five of which were new for this group (Nowińska & Brożek, 2019).

### Hygro-thermoreceptive sensilla

Various kinds of sensilla are described and defined in the hygro-thermosensitive sensillar system (Altner & Prillinger, 1980). Usually, sensilla hygro-thermosensitive appear as small aporous cuticular pegs (i.e., sensilla coeloconica) originating from the antennal surface or set in pits (sensilla ampullacea) (Tichy & Kallina, 2013). Generally, water bugs fly from one body of water to another during mating season or to find new water habitats. They can also disperse in other ways (Wróblewski, 1980). Temperature and humidity are major determinants of distribution patterns for species. In Gelastocoridae, some species are not able to fly (due to fused hemelytra) and in others flight has not been observed, but nonetheless these species are frequently found away from water. It seems like this kind of hygro-thermosensitive sensilla is essential for finding other water reservoirs (Chen et al., 2005). This might explain the presence of several sensilla ampullacea and sensilla coeloconica in the studied species. In *Aphelocheirus*, which happens to be the only species living submerged, numerous sensilla ampullacea occur. These have been found along with sensilla SPL, on the last antennomere. However, several sensilla coeloconica (SCo) have also been found in species of Gelastocoridae and Ochteridae, localized mainly on the 3<sup>rd</sup> and 4<sup>th</sup> antennomeres. Moreover, sensilla ampullacea were in different locations throughout the antennae in these taxa. In Nepoidea, sensilla coeloconica (three subtypes) with the same structure also occurred (Nowińska & Brożek, 2019). Therefore, we cannot exclude the potential hygro-thermoreceptive function of sensilla ampullacea and coeloconica. Moreover, these sensilla, especially sensilla coeloconica, are aporous sensilla with inflexible

sockets and few in number. According to Altner (1983), such morphological characters of the sensilla represent one fundamental sensillum type and their structural features can be regarded as adaptations to hygro- and thermoreception. The bimodal hygro-thermoreceptive sensilla exhibited the strongest responses to changes in humidity as well as temperature changes, because the moist cells' and the dry cells' discharge rates increase with high temperatures. This phenomenon was observed i.e., in *Periplaneta americana* (Tichy & Kallina, 2013).

### *Comparison to the other heteropteran groups*

It is significant that within Nepomorpha there are two types of antennae. In Ochteridae and Aphelocheiridae the antennae are long and extend over the head, making them very similar to the long and thin antennae in Gerromorpha and other heteropterans (Andersen, 1982; Shuch & Slather, 1995), while in Nepoidea, the antennae are short and concealed beneath the head, as in Gelastocoridae (La Rivers, 1953; Menke, 1979; Zettel & Lane, 2010). Nonetheless, both types of antennae involve complex sensilla of different modalities and appearance, despite a common underlying architecture.

Generally, a sensillar system is conserved throughout the different insect orders, making it improbable that these different types of sensilla have evolved independently several times (Steinbrecht, 1997). That is probably why a similar set of functional sensilla is observed in terrestrial and aquatic heteropteran insects.

However, the adaptive value of conserving both types of olfactory sensilla ('single-walled wall-pore', 'double-walled wall-pore') throughout almost all insect taxa to date requires further verification (Steinbrecht, 1997). The sensory peg of the double-walled sensilla is smooth at the base and has a grooved cuticular



surface distally, with pores organized in spoke channels between each ridge, in contrast to the single-walled sensilla with a porous thin cuticular wall. Also, sensilla basiconica distinguished in the presently studied water taxa, belong to both 'single-walled wall pore' (SB2, SB3) and 'double-walled wall pore' classes (SB4). Olfactory sensilla basiconica (SB2) are present in all studied taxa and the remaining sensillar types (SB3, SB4) have different configurations according to subfamilies/species. In the studied taxa, sensilla ampulacea (SA), campaniformia (SCa) and trichoidea (ST2) belong to a standard set of sensilla, just like SB2. Probably, these sensilla (SB2, ST2, SA, SCa) originated from the protoheteropteran line and retain plesiomorphic sensillar features. Hence, we observe some common features of Ocherioidea and Aphelocheiridae with Nepoidea. Among the other types of sensilla, significant changes in their shape, size and distribution were demonstrated in the studied taxa. Sensilla placodea (usually olfactory) are not common in nepomorphan taxa (except Aphelocheiridae), as sensilla placodea multilobated are characteristic of one family (Gelastocoridae). In Nepoidea, however, sensilla coeloconica (subtypes 1, 2, 3) were recognized as multiporous chemoreceptive sensilla (Nowińska & Brożek, 2019), whereas in the presented taxa, sensilla coeloconica are recognized as hygro-thermoreceptive sensilla. Other heteropteran taxa/species display a presence of multiporous sensilla basiconica or trichodea ('single-walled wall-pore', 'double-walled wall-pore') on the antennae, while sensilla placodea are rarely present. However, often their shape, size and number are slightly varied, like in reduviids (Catalá, 1997; Gracco & Catalá, 2000; Guerenstein & Guerin, 2001; Carbajal de la Fuente & Catalá, 2002; Slu, 1980), miriids (Chinta et al., 1997), Alydidae (Rani & Madhavendra, 2005; Ventura & Panizzi, 2005), lygaeids (Rani & Madhavendra, 2005), pentatomids (Rani & Madhavendra, 1995; Brézot

et al., 1997; Sinitsina & Chaika, 1998; Ahmad et al., 2016), coreids (Akent'eva, 2008) and in Gerromorpha (Nowińska & Brożek, 2017). The thermo-hygroreceptive sensilla found in the studied families (ampulacea or aporous sensilla coeloconica) are mostly the same types and functions, although their size and how they are embedded is different. Aporous sensilla coeloconica on the flagellum can also be regarded as playing a thermo-hygroreceptive role, in other insects/heteropteran species: *Nezara viridula* (Pentatomidae), *Odontopus nigricornis* (Pyrrhocoridae), *Cyclopelta siccifolia* (Dinidoridae), *Chrysocoris purpureus* (Scutelleridae), *Piezodorus guildinii* (Pentatomidae), *Leptoglossus zonatus* (Coreidae) as well as in some gerromorph species (Usha Rani & Madhavendra, 1995, 2005; Brézot et al., 1997; Chapman, 1998; Silva et al., 2010 Ruchty, 2009; Gonzaga-Segura et al., 2013 Nowińska & Brożek, 2017; Schneider, 2018). For terrestrial heteropteran insects, another common type of mechanoreceptive sensilla is sensilla trichodea, but usually in different lengths and even distributions on all antennomeres, similar to mechanoreceptive sensilla basiconica. Sensilla chaetica are less numerous than sensilla trichodea and are sparsely distributed or only occur as single structures in different terrestrial heteropteran taxa. Sensilla campaniformia show a uniform structure in all mentioned taxa (Chinta et al., 1997; Slu, 1980; Akent'eva, 2008; Ahmad et al., 2016; Nowińska & Brożek, 2017).

Ochteridae is more connected with terrestrial environments (Andersen & Weir, 2004), therefore similarities with the antennal sensilla of terrestrial Heteroptera could have been expected, which is different from what is observed in Gelastocoridae and Aphelocheiridae. Present studies have shown that the main sets of antennal sensilla in these three families (table 1, fig. 6) are generally similar to those in Nepoidea – insects submerged in water. Multiple types of mechanoreceptive

and chemoreceptive sensilla were documented in all of them. Sensillum club-like, which was new for Nepoidea, was also observed during the presented studies and sensilla ampullacea works as the main thermo-hygroreceptive sensillum for all the families in Nepoidea as well as within the presently studied species.

The main difference between nepoid groups (six types of mechanoreceptive sensilla in Belostomatidae and seven types in Nepidae) (Nowińska & Brożek, 2019) and the families mentioned above, is the fewer amount of mechanoreceptive sensilla types (three: trichodea, chaetica and campaniformia). These differences in structure/types of sensilla in particular taxa show how sensory systems have adapted to new lifestyles, and future studies on other nepomorphan families may show further new features.

### *Short phylogenetic remarks for studied groups*

In the present study, the antennal sensilla (ST<sub>1</sub>, ST<sub>2</sub>, Sch, SB<sub>1</sub> SB<sub>2</sub>, SCa, SCo) are presumably plesiomorphic, due to having the same shapes and similar distributions of the sensilla as reported in Nepoidea (Nowińska & Brożek, 2019) – the superfamily considered to be the primary taxon of Nepomorpha (Popov 1971, Hebsgaard et al., 2004, Brożek, 2014).

On the other hand, sensilla placodea multilobated (SPM) have been reported only in the species of Gelastocorinae and Nerthrinae and probably represent an evolutionary novelty for them, therefore being synapomorphic.

Sensillum basiconicum (SB<sub>4</sub>) has been observed only in ochterid and gelastocorid species and is a synapomorphic feature of Gelastocoridae and Ochteridae, and therefore, a confirmation of their close relationship. There is more evidence to suggest a close relationship between Gelastocoridae and Ochteridae, which together compose Ochteroidea (Hebsgaard, et al., 2004). The presence of sensilla

plate-like (SPL) only in Aphelocheiridae, on the other hand, indicates an autapomorphy.

Currently and according to expectations, we have not found any signs indicating a relationship between Ochteroidea and Aphelocheiridae, because the taxon is quite distant from the family. Future study of antennal sensilla in naucoroid species may be of importance when it comes to phylogenetic considerations.

### **Conclusions**

The studied families show variations in their adaptation to aquatic habitats, as well as in antennae's shapes. The basal set of sensilla (ST<sub>2</sub>, SCa, SB<sub>2</sub>, SA) is similar in all of them and is not different from the sensilla present in Nepoidea (ST<sub>2</sub>, SCa, SB<sub>2</sub>, SA). They share the same type of sensillum (SCIL) which is new to Nepomorpha, and all of the studied families, as well as Nepoidea, use mainly sensilla ampullacea for thermo-hygroreception. On the other hand, the shapes of antennae and sets of sensilla in the studied families of Nepomorpha are different compared to semi-aquatic bugs (Gerromorpha). There are more sensilla subtypes in Gerromorpha (18) and their antennae are very long and thin, while the antennae of the studied species bear fewer types of sensilla, are much shorter and, in some species (Gelastocoridae), concealed beneath the eyes. The antennae of Aphelocheiridae bear sparsely distributed sensilla, which are mostly sensilla basiconica. It is possible that the number of sensilla has been reduced because of their preference for running water habitats. The antennae of Ochteridae and Gelastocoridae are mostly covered by sensilla trichodea, with lone sensilla basiconica and coeloconica sparsely distributed on the surface. There were two types of thermo-hygroreceptive sensilla present in the families – sensillum ampullaceum and sensillum coeloconicum. New

types of sensilla, characteristic of the antennae of Aphelocheiridae (SPL) and Ochteroidea (SPM), have also been found. This supports our hypothesis that the antennal sensilla of the studied families reflect their different adaptations for use in aquatic habitats, while maintaining a common set of sensilla similar to other nepomorphan insects. The study also confirms the systematic position of Ochteridae as closely related to Gelastocoridae. Antennal sensilla of Naucoroidea will be studied in the future. Therefore, we expect to compare present results of Aphelocheiridae with other species of Naucoroidea and apply a cladistic method for a more thorough assessment of their phylogenetic significance.

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